2. PATTERNS IN POST-DISPERSAL SEED REMOVAL BY NEOTROPICAL RODENTS AND SEED FATE IN RELATION TO SEED SIZE

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SUMMARY

1 Animals are important agents of seed dispersal and plant recruitment in the tropics. Currently, it is generally assumed that seeds removed after primary dispersal are doomed by predation; the probability of secondary dispersal and further escape is seldom ascertained.

2 This chapter reports experiments that were carried out on Barro Colorado Island, Panama, to test the effect of seed size (>1 cm) and weight (>0.1 g) on the level of removal and fate for several tree species illustrating a variety of seed size and dispersal syndromes.

3 Seed fate was explored in the context of the habitat in which seeds land. Two habitats were recognized based on the frequency of agoutis observed along one transect across the forest: one agouti-rich area located close by the young forest, and one agouti-poor area further in the old forest.

4 Patterns of seed removal as well as the fate of small to large seeds, especially the probability of seed caching, changed between species and habitat depending on seed reward.

5 Small seeds (≤1 g weight and *c.* 1 cm long) had a low probability of being missed by vertebrates, and there was no effect of the visitation rate of agoutis. Removal by terrestrial mammals mostly accounted for predation although the seeds of *Eugenia* (1.2 g) were cached by rodents more frequently (12%) than those of *Cupania* (0.2 g; 2%) and *Doliocarpus* (0.7 g; 0%).

6 Among medium seeds (*c.* 1–3 g and 1–2 cm), the habitat and the quality of seed nutrient reward in cotyledons differentially affected removal and fate. High removal in *Brosimum* seeds (2.2 g) with edible cotyledons corresponded to either predation or caching. On the contrary, removal in *Virola*

seeds (3 g), with toxic cotyledons, accounted for caching more frequently. Greater burying rates occurred in *Virola* where agouti sightings were lower.

7 Among large seeds (*c.* >3 g and >2 cm), fate was independent of habitat and month for the large nutrient-rewarding *Gustavia* seeds (12 g) only, seeds of which were more often buried than the less nutrient-rewarding *Licania* seeds (6 g). In the latter predation was dependent on habitat and month.

8 Similar patterns of seed removal mean contrasting seed fate pathways depending on seed size: a gradient of caching rate was observed from smaller to the larger seeds. Change in caching rate is assumed to be related to change in agonistic and caching behaviour among agouti populations which vary in density. A method of seed labelling is therefore essential to conclude whether rodents are effective seed dispersers.

INTRODUCTION

Seed dispersal by flying and arboreal frugivorous vertebrates dominates in neotropical rainforests (Janzen 1970, Howe & Smallwood 1982, Howe 1986). Seedfall patterns change depending on the spatial distribution of fruiting trees and seed attributes such as seed size that determine the guild of seed dispersers. The density of fruiting trees and the seasonal occurrence and abundance of fruits and alternative resources (insects and leaves) also affect how frugivores forage and behave, and likely determine where and how seeds will be deposited in the forest (Schupp, Howe, Augspurger & Levey 1989), scattered or clumped (Howe 1989). Post-dispersal removal of seeds often follows initial dissemination by animals and varies between species, on spatial and temporal scales as a function of habitat and forest types, food abundance and the community of predators (e.g. Schupp 1988a,b, Willson 1988, Osunkoya 1994) some of which may behave as dispersers (Janzen 1971a, Chambers & MacMahon 1994). The probability of seedling establishment will then be contingent on whether seeds are harvested or ignored, consumed or cached, and in this latter case retrieved or abandoned by either invertebrates, especially ants (e.g. Byrne & Levey 1993, Kaspari 1993, Levey & Byrne 1993) or vertebrates, mostly rodents (Price & Jenkins 1986, Forget & Milleron 1991, Crawley 1992, Terborgh, Losos, Riley & Bolanos Riley 1993, Terborgh & Wright 1994). Currently, the fate of those seeds that disappear is unknown and it is generally assumed that they are doomed to predation; the probability of secondary dispersal and further, of escape, is seldom ascertained. Seed fates need to be examined with reference to seed size and mode of primary dispersal, in the context also of the habitat in which the seeds land.

A preliminary approach to assessing rodent impact on the seedling establishment is to outline the possible pathways to different seed fates (Price & Jenkins 1986). Price and Jenkins's (1986) seed fate pathway diagram is useful for formulating hypotheses and then for designing experiments to test for the spatial and temporal effects of factors related to both seeds and rodents. Seed pathways are multiple, most of them leading to death but, in some instances, to seedling establishment. When seeds remain undispersed above ground they are often killed by vertebrate and invertebrate predators. Uncached seeds may germinate if their toxicity saves them from consumption by animals. Despite secondary dispersal (i.e. dispersal by terrestrial animals following primary dispersal by arboreal and/or flying animals), scatter- or larder-hoarded seeds (Morris 1962) may die in the caches due to pre-dispersal infestation, drought, pathogens or mammals that dig up the cotyledons before or after seedling establishment. Seeds may be retrieved quickly and recached further away by the same or another rodent (P.-M. Forget & T. Milleron, personal observation). Though poorly documented, such complex pathways may be more common than previously thought. Seedling establishment follows dispersal when seeds hidden in caches, and protected from post-dispersal predators, are abandoned or forgotten by cachers and not recovered by other predators.

When questioning the significance of seed removal by rodents, it is essential to know what internal and/or external factors trigger seed predation or dispersal (Vander Wall 1990). Extrinsic factors related to habitat, such as the availability of alternative seed resources (e.g. Forget 1992) and the animal community (for example, Osunkoya 1994), and intrinsic factors related to seed attributes, such as size, chemistry and nutrient content reward in cotyledons (e.g. Rankin 1978), control the level of seed harvesting by terrestrial animals (Price & Jenkins 1986, and references therein). Depending on habitat choice and rodent foraging activity within a given habitat, one might expect the level of seed removal and predation to change between and within species, as shown in several studies (Rankin 1978, Boucher 1981, De Steven & Putz 1984, Sork 1987, Schupp 1992, 1995, Osunkoya 1994). High seed removal in species that are strictly dependent on rodents for dispersal probably reflects high levels of scatter-hoarding (Forget 1992, 1996), whereas other abiotically dispersed species' seeds may be exclusively eaten (Rankin 1978, Forget 1989). Seasonal spatial distributions of resources may govern the probability that seeds will be harvested, consumed or dispersed by rodents (Hallwachs 1986, Forget 1993, Forget, Munoz & Leigh 1994). Seeds that are removed rapidly in the dry season, in general when food availability is low, will often be more predated than in the wet season (Rankin 1978, Hallwachs 1986).

Not only large-seeded species but also a wide range of species whose seeds offer small or intermediate nutrient rewards are removed and fall prey to small ground-dwelling vertebrates (Fleming 1974, Vandermeer 1979, Vandermeer, Stout & Risch 1979, Emmons 1982, Smythe, Glanz & Leigh 1982, Dirzo & Dominguez 1986, Larson & Howe 1987, Schupp 1988a,b, 1990, Chapman 1989, Schupp & Frost 1989, Zona & Henderson 1989, Estrada & Coates-Estrada 1991, Burkey 1993, 1994, Howe 1993, Hammond 1995). Small- and medium-sized seeds are cached by either small or large rodents, and this hoarding activity varies between rodent species, month, season and habitat (Fleming & Brown 1975, Forget 1991, 1993, Forget & Milleron 1991, Hallwachs 1994, Hammond 1995, Asquith, Wright & Clauss 1997). The smallest seeds, easy to handle and with the lowest energetic value will be most likely consumed by mice (which weigh <100 g), or discarded if they contain alkaloids toxic to mammals (Price & Jenkins 1986). Seeds with larger nutrient rewards will be either scatter-hoarded or eaten by spiny rats (250–500 g) and dasyproctid rodents (1–6 kg) (Emmons & Feer 1990), or discarded. Given a similar seed size, high-quality seeds should be harvested more often than low-quality seeds (Price & Jenkins 1986). The impact of small vertebrates on seed fate awaits further research, especially when the animals encounter and harvest seeds that have been dispersed already by other animal species (see Janzen & Martin 1982, Hallwachs 1986).

This chapter reports experiments that were carried out in Panama to test the effect of seed size on removal and fate for several tree species, illustrating a variety of dispersal syndromes. Several questions are addressed: how does seed fate change as a function of seed size? To what extent do some tree species depend on secondary seed dispersal by rodents? How does seed fate change across rodent population density gradients within a forest? Does the rate of caching change during the fruiting season?

STUDY SITE AND AREA

The study site is the tropical moist forest of Barro Colorado Island (BCI) (Leigh, Rand & Windsor 1982). BCI is covered with forest stands varying in age from relatively young (*c.* 100 years) to very old (*c.* 500 years) (Foster & Brokaw 1982, Piperno 1990). The climate of BCI is seasonal with a well-marked dry season of variable length and intensity, lasting from December or January to April, and a wet season for the rest of the year with a peak in rainfall in October–November (Rand & Rand 1982). There are two peaks in fruiting: in April–May (wind and animal dispersed species) and again in September–October (animal dispersed species) (Foster 1982). Because of habituation to humans, the BCI rodent community changes between forest habitats depending on the distance from the laboratory (Wright, Gompper & De Leon 1994). The results of Wright *et al.* (1994) led us to analyse spatial–temporal seed removal and fate by considering the number of diurnal rodent encounters along a trail within the study area. In the rodent community, an agouti (*Dasyprocta punctata*) ranks first in sighting counts, followed by a squirrel (*Sciurus granatensis*) (agoutis being about five times more sighted than squirrels) and then a paca (*Agouti paca*). Population levels of small rats such as spiny rats (*Proechimys semispinosus*) and mice (*Oryzomys* spp.) fluctuate widely from year to year in French Guiana, for instance (S. Ringuet personal communication, P.-M. Forget personal observation) as is also probably the case on BCI. Spiny rats were rarely observed by Wright *et al.* (1994) during nocturnal censuses while they may be much more abundant on BCI in other years (D.C. Tomblin & G.H. Adler, personal communication). In 1990, spiny rats were rarely seen on the study trail and seeds did not disappear at night during the first days of the experiments in the dry season (Forget 1993, P.-M. Forget personal observation) as well as in the wet season during this study (see Results). As a consequence, because of its large body size and abundance on BCI, as well as its food preference for the tested plant species (Smythe *et al.* 1982), agouts are assumed to have been responsible for most of the caching in 1990.

The study was undertaken in June–August 1990 along the R.C. Shannon trail between the 100- and 700-m trail markers (see Fig. 1 in Forget 1993). The study period coincided with the mid-wet season when food was abundant for rodents and preceeding the onset of food scarcity during August–March (Smythe 1970, 1978). The forest was classified as old but was close to a patch of young regrowth (Fig. 5 in Foster & Brokaw 1982, R. Foster personal communication). The diurnal rodent community was checked during monthly strip censuses (n = 10 per month) between November 1989 and May 1990. An animal was recorded when it was visible at a distance of *c.* 15–20 m on each side of the trail; distant alarming rodents were not counted if not within the range of visibility in the understorey. Agoutis (n = 146) accounted for more than 90% of all diurnal rodent sightings (n = 160) along the study trail. Agouti sightings changed from month to month, especially between February and April, presumably as a function of food availability in the area of the study trail (Forget 1993). Averaging the data for the entire 6-month period prior to experimentation, there was a decrease in the frequency of agoutis along the trail (Fig. 2.1), the greatest frequency being observed close to a patch of young tall forest surrounding the laboratory area, as shown by Wright *et al.* (1994). The decline in agouti sightings near the 250-m trail mark corresponds to a ravine where agoutis were rarely observed — one pair of agoutis lived on each side of the ravine. A

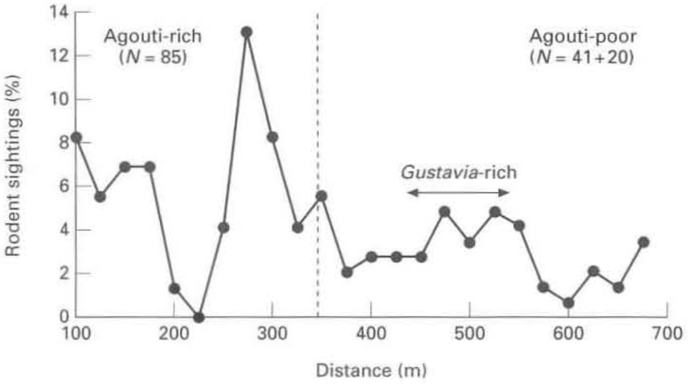

FIG. 2.1. Frequency of rodent sightings along the R.C. Shannon Trail on Barro Colorado Island, Panama, between November 1989 and May 1990. Definition of the two forest areas was based on the distance to trail origin, as an agouti-rich area at 100–325 m distance classes, and an agouti-poor area further away. One part of the trail (*Gustavia*-rich) was not used during the study of seed fate. Total number of agoutis encountered per transect section are shown in parenthesis; 20 animals were seen along the 100-m section at *Gustavia*-rich area, and 41 along the rest of the trail at the agouti-poor area.

greater density of key resources for agouti, such as *Dipteryx panamensis* and *Astrocaryum standleyanum* at the beginning of the Shannon Trail (Forget 1993; P.-M. Forget & T. Milleron personal observation) near the young forest, most probably accounted for the skewed rodent density versus the other part of the trail. Two forest areas were thus defined based on distance to origin of trail: an agouti-rich area at 100–325 m distance, and an agouti-poor area further away. A limit (>350 m) between the two zones was arbitrarily set to achieve equal numbers of seed piles (n = 10) per area for the experiments. Because another experiment was carried out in the area around the trail with an abundant population of *Gustavia superba* trees (the *Gustavia*-rich area in Forget 1992), as shown in Fig. 2.1, this part of the trail was not used for the present study.

STUDY SPECIES

The study species were the liana *Doliocarpus olivaceus* Sprague & L.O. Wms. ex Standl. (Dilleniaceae) and the trees *Cupania latifolia* H.B.K. (Sapindaceae), *Eugenia coloradensis* Standl. (Myrtaceae), *Brosimum alicastrum* Sw. subsp. *bolivarense* (Pitt.) C.C. Berg (Moraceae), *Virola nobilis* A.C. Smith (Myristicaceae), *Licania platypus* (Hemsl.) Fritsch (Chrysobalanaceae) and *Gustavia superba* (H.B.K.) Berg (Lecythidaceae)

TABLE 2.1. Seed features, characteristics of the experimental design and mean (SD) percentage of seeds removed for each species per study month in 1990 on Shannon Trail at Barro Colorado Island, Panama.

Species	Seed weight (g) ($n = 30$)	Seed length (cm)	Study month	No. seeds per clump × no. sites	No. days per experiment	Removal (SD) %
Doliocarpus	0.21	1.1	August	5 × 20	1	91
Cupania	0.74	1.1	August	5 × 20	1	100
Eugenia	1.27	1.3	August	5 × 20	1	96
Brosimum	2.24*	1.8†	June	5 × 20	28	86
Virola	2.95	2	June	5 × 20	42	52
Licania	6.3	2.4	July	10 × 20	14	100
			August	10 × 19	1	99
Gustavia	12.6	1–3.5	June	10 × 20	28	88
			July	10 × 20	28	100

* S.J. Wright, personal communication ($n = 25$ seeds).
† Estrada & Coates-Estrada (1986).

(Table 2.1). Hereafter they are referred to by their genus in the text, table and figures. Nomenclature follows Croat (1978) except for *Virola* (Forget & Milleron 1991). In Table 2.1, these species are ranked by increasing seed weight. The first five species are likely to be dispersed by arboreal mammals, especially monkeys, and birds (Howe & Vander Kerkhove 1980, Oppenheimer 1982, Estrada & Coates-Estrada 1984). Peeled *Licania* seeds were observed beneath the palm fronds (P.-M. Forget personal observation) which are often used by bats as feeding roosts. Lacking large fauna to ingest the entire fruit (Janzen & Martin 1982, Howe 1986), *Gustavia* seeds are dispersed by scatter hoarding rodents (Forget 1992; see also Hallwachs 1986). All study genera are also consumed by spiny rats (Guillotin 1982, Adler 1995) which may also scatter the hoard seeds intensively (Forget 1991) when they occur at high densities on BCI (D.C. Tomblin & G.H. Adler personal communications).

METHODS

Experimental design

One clump of seeds cleaned of the arils or remains of pulp was placed at each of 20 sites within 2–5 m of the study trail, each seed set (pile) being separated by a 25-m interval; 10 clumps were set in the agouti-rich area and 10 clumps in the agouti-poor area. Clumps of 5–10 seeds were used in order to simulate clumped seed dispersal by frugivores (Howe 1989) beneath roost and perching trees. Clumps were made in sets of five seeds (areas of 50 × 50 cm; two sets 1 m apart in *Licania* and *Gustavia*) positioned each like a die-face number 5. To avoid further lateral movement, seeds were placed in a superficial depression in the ground, made with the thumb, and the location of each seed was marked with a wooden stake. Each seed was tagged with a 60-cm thread passing through it, which allowed the seed's fate to be followed, i.e. whether it was eaten, cached or lost (not found), after relocation of the thread with the intact cached seed or remains of the gnawed seeds (Forget 1990). In contrast to the spool-and-line method in which labelled seeds are attached to a fixed point (see Soné & Kohno 1996), rodents were allowed to move free thread-marked seeds long distances (>30 m). Seeds were retrieved, however, within 5 m for all species, except for *Licania* and *Gustavia* where the distance was up to 10 m. *Cupania*, *Doliocarpus* and *Eugenia* seeds were deposited mixed and simultaneously on 27 August 1990. Experiments with *Brosimum* and *Virola* seeds started on 14 and 29 June, respectively. *Licania* seeds were set on 27 July and 22 August, and *Gustavia* seeds on 21 June and 17 July. The number of days the experiment lasted differed between species depending on the time needed for all seeds to be removed, or for them to germinate or to rot (Table 2.1). Among *Cupania*, *Doliocarpus*, *Eugenia* and *Licania*, high seed removal occurred in the daytime within 12 h, and remained constant thereafter. The results only consider data collected after 1 day. Comparing medium-sized and large-sized seed species required consideration of the time needed for seeds to germinate (<4 weeks for *Brosimum* and *Gustavia*) or to rot (4–6 weeks for *Virola*) when not removed by animals. The data for *Virola* are from Forget and Milleron (1991) at the *Virola*-rich habitat (areas 1 & 2), and are presented here differently for comparison with *Brosimum*. The effect of month on seed fate was tested for *Licania* and *Gustavia* only.

Statistical analysis

The experiment conformed to a split-plot factorial design; the design had one between-block treatment (habitat: agouti-rich and agouti-poor areas; fate: eaten, cached and lost) and one within-block treatment (species) (see Kirk 1969, p. 247). Percentage of seeds removed and percentage of seeds in each fate category were based on the total number of seeds deposited per pile. Percentages were compared between species with similar seed size (small in *Doliocarpus*, *Cupania* and *Eugenia*; medium in *Brosimum* and *Virola*; large in *Licania* and *Gustavia*) and between months (June and July in *Gustavia*; July and August in *Licania*) using two- and three-way fully crossed

ANOVAs in PCSM-Plus V6.3 statistical package (PCSM 1994) after arcsin square-root transformation of the data (Sokal & Rohlf 1981). We wanted to address whether percentages in each fate category differed between habitats and species, and whether there were any interactions between these factors. Analysis allowed us to test for between-block variability due to the factor habitat and within-block variability due to the factor species, to the interactions of habitat and species, and of the two factors with error term different for each interaction (PCSM 1994).

RESULTS AND DISCUSSION

Change in seed fate: small-sized seeds

In August, seed removal was almost complete within 1 day (i.e. 12 h) for *Doliocarpus*, *Cupania* and *Eugenia* (Table 2.1). Neither species nor habitat (agouti-rich vs. agouti-poor area) or the interaction of species and habitat significantly affected the level of seed removal ($P > 0.19$). Similarly, neither habitat nor the interaction of habitat with species affected the percentage of seeds per fate category ($P > 0.69$). There was a significant effect of the species on seed fate (eaten: $F_{2,36} = 11.35$, $P = 0.0001$; cached: $F_{2,36} = 5.01$, $P = 0.012$; lost: $F_{2,36} = 3.62$, $P = 0.037$). Despite a similar seed size (*c.* 1 cm in their greatest dimension), the heavier seeds of *Eugenia* were observed cached more frequently (12%) than the lighter seeds of *Doliocarpus* (2%) and *Cupania* (0%) which were both essentially destroyed by the predators (Fig. 2.2).

Seeds as small (<1 g) as *Doliocarpus* and *Cupania* had a low probability not to be harvested by ground-dwelling vertebrates, and removal mostly meant predation by rodents. Because there was no effect on agouti density, removal and predation may have been due to small rodents such as spiny rats which may have been more abundant than previously thought on BCI (D.C. Tomblin & G.H. Adler personal communication). However, since most seeds disappeared at daytime (between 06:30 and 18:30), agouti and possibly squirrels were the main predators.

The experiment started in early August; that is, before the peak availability of small seeds 0.1–1 g, and when there were few large seeds in the forest (Foster 1982). By September–October, large rodents would be expected to be disinterested in such nutrient-poor seeds and be preferentially searching for more rewarding large seeds and caches (Smythe 1989, Forget 1992, Forget *et al.* 1994). One may postulate that removal of small seeds should decrease and fewer seeds should be consumed during September–October fruitpeak (see Foster 1982). At the same study area, with a comparable

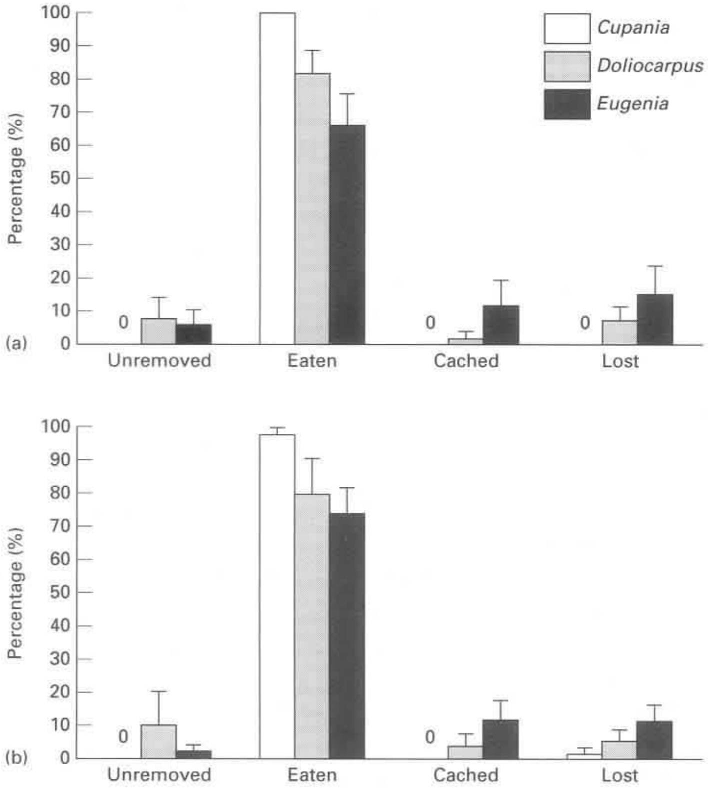

FIG. 2.2. Percentage of seeds (20 sites × 5 seeds) unremoved and the fate (eaten, cached or not retrieved within 5 m: lost) of removed seeds of *Doliocarpus*, *Cupania* and *Eugenia* in August 1990 at (a) the agouti-rich area and (b) the agouti-poor area along along the R.C. Shannon Trail on Barro Colorado Island, Panama. Bars = 1 SE of mean.

rodent community, Schupp (1988a,b, 1990) described the survival function of *Faramea occidentalis* (Rubiaceae) seeds that weighed 0.29 g on average. Within 4 weeks, seed removal ranged approximately 25–55% across four different years (Schupp 1990), and the survival probabilities of seeds were positively correlated with distance away from the parent tree in the understorey (Schupp 1988a,b). Because he carried out his experiment in January on BCI, that is, in the late wet to early dry season when overall food was scarce in the forest, Schupp (1988a) considered seed removal to be primarily due to seed predation. None the less, agoutis may occasionally bury *Faramea* seeds in November–December in the vicinity of parent trees (P.-M. Forget personal observation). Spiny rats which are known to consume *Faramea* seeds (Adler

1995) are also potential seed dispersers caching seeds below the litter and near logs (Forget 1991, Hoch & Adler 1997). Dirzo and Dominguez (1986) observed contrasting seed removal rates in *Trichilia martiana* (Meliaceae) between microhabitats in Los Tuxtlas, Mexico, and questioned the significance of these results given the possibility of secondary seed dispersal. Hammond (1995) found that on-site predation was less important than removal in *Erythrina goldmanii* (Fabaceae), *Spondias mombin* (Anacardiaceae) and *Bursera simaruba* (Burseraceae) weighing 0.21, 0.86 and 0.86 g, respectively. Local burial (<1 m) was evidenced in *Spondias*, and was of greater importance than predation. On the contrary, on-site predation was dominant in *Swietenia humilis* (Meliaceae) whose seeds weigh 0.80 g (Hammond 1995).

According to our results and Hammond's (1995) study, removal nearly equals predation by both small and large rodents when seeds weigh less than 1 g, especially when seeds are neither infested by insects after dispersal nor require burial for germination. Consequently, survival probability is exclusively dependent on patch suitability for seedling establishment and growth once seeds escape predators (Howe & Smallwood 1982, Schupp 1995). Seed survival rate through seedling establishment varies as a function of both spatial and temporal factors. On the one hand, survival may be related to either rodent density (Osunkoya 1994) or fruit tree density (Schupp 1992). On the other hand, selective pressures applied by different rodent species might be constrained by seasonal and year-to-year changes in either specific or plant community food availability depending on overall habitat richness. Regardless of the level of predation, the real impact of rodents as seed-eaters should be considered with caution for seeds nearly or greater than 1 g (as in *Eugenia*), which were secondarily scatter hoarded by rodents within 5 m (see also Hammond 1995).

Change in seed fate: medium-sized seeds

In June, seed removal rate was greater for *Brosimum* than for *Virola*, and there was a significant interaction of habitat and species on level of seed removal ($F_{1,18} = 18.47, P < 0.0001$). *Virola* seed removal rate was significantly greater ($F_{1,19} = 18.42$, $P < 0.001$) at the agouti-poor area (78%) than at the agouti-rich area (26%) while there was no difference ($P > 0.05$) for *Brosimum* (88 and 84%, respectively). The interaction of species and habitat was significant for each fate category (eaten: $F_{1,18} = 10.29, P = 0.0049$; cached: $F_{1,18} = 14.06, P = 0.0012$; lost: $F_{1,18} = 14.10, P = 0.0014$). In *Brosimum*, 58% of the seeds were recovered gnawed at the agouti-poor area whereas seeds were more frequently buried (26%) or lost (40%) at the agouti-rich area

(Fig. 2.3). Trends were different for *Virola*. Seeds were cached (42%) or lost (28%) at the agouti-poor area and remained largely unharvested at the other area (Fig. 2.3). In comparison to *Virola*, *Brosimum* seeds were a much preferred food item for rodents in general.

In Central America, *Brosimum* is an important primary source of fruit for howler monkeys (*Alouatta palliata*) that disperse seeds in clumps, on average up to several hundred metres away from parents (Estrada & Coates-Estrada 1984). Whether or not seeds are left in dung or fall beneath the parent tree does not affect germination rate but, based on seedling counts and survival under the tree crown, seeds that are dispersed are likely

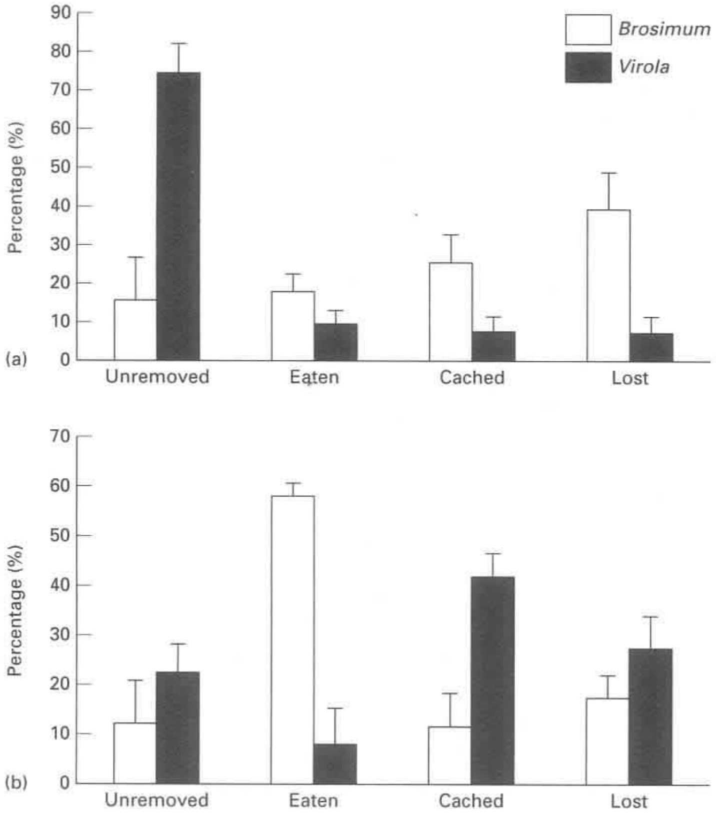

FIG. 2.3. Percentage of seeds (20 sites × 5 seeds) unremoved and the fate (eaten, cached or not retrieved within 5 m: lost) of removed seeds of *Brosimum* and *Virola* in June 1990 at (a) the agouti-rich area and (b) the agouti-poor area along along the R.C. Shannon Trail on Barro Colorado Island, Panama. Bars = 1 SE of mean.

to escape intense post-dispersal predation by mice (Estrada & Coates-Estrada 1991). Burkey (1994) found that *Brosimum* seed removal rate was negatively correlated with seed density but not at short distances (5–25 m) to the parent tree. He suggested that predator satiation was more important than dispersal distance in reducing the impact of seed-eaters. However, at Burkey's study site, close to a road that was human-disturbed and likely to have been in a hunted area, agoutis might have been less represented in comparison to small rodents such as Mexican deer mouse (*Peromyscus mexicanus*) and spiny pocket mice (*Heteromys desmarestianus*) (see Estrada, Coates-Estrada & Meritt 1994). In Los Tuxtlas, these two mice are the main consumers (Estrada & Coates-Estrada 1991) and potential scatter hoarders of *Brosimum* seeds (Fleming & Brown 1975, Emmons & Feer 1990). Therefore, it is probable that the contrast between low removal rate (40% after 20 days) reported by Burkey (1994) and higher values (100 and 88% after 10 and 2 days, respectively) in Estrada and Coates-Estrada (1986, 1991, respectively) and this study (86% after 28 days) was due to differences in rodent populations between habitats and this is likely to have been the result of the edge effect in a fragmented forest (Burkey 1993, Murcia 1995; see also Hammond 1995).

Seed removal by vertebrates in *Virola* is likely to be more influenced by tree neighbourhood, especially mean crop size (as in *Brosimum*, Burkey 1994), than by distance which instead affects seed damage by bruchids (Howe, Schupp & Westley 1985, Howe 1993). We observed that greater seed removal, associated with high caching rates in *Virola*, occurred where agouti sightings were lower. Change in agouti behaviour between areas may explain such a result. Korz, Heindrichs & -Militzer (1996) observed that captive male agoutis (*D. punctata*) living in pairs were more often burying food and scraping the ground with their forefeet (to retrieve food and to bury) than other males living in large groups with several females. As suggested before for *Brosimum*, *Virola* seed fate is also likely to be altered by forest age. In both *Brosimum* and *Virola*, seed fate changes widely across forested habitats, possibly in relation to the ground-dwelling vertebrate community. Osunkoya (1994) showed that survival of diaspores was lower in a forest with the greatest abundance of rodents. Hoch and Adler (1997) found that the proportion of *Astrocaryum standleyanum* palm seed disappearing was dependent on the density of spiny rats on islands in Panama. The contrast in the proportion of seeds removed on the one hand, eaten or buried on the other hand, should then be correlated with the density of either small or large rodents across a diversity of habitats ranging from small and large islands to the mainland (Gliwicz 1984, Adler & Seamon 1991).

Although agoutis and other smaller rodents on BCI and mice in Los Tuxtlas may retrieve their hoards as well as seeds transported 2–5 cm deep by beetles (Estrada & Coates-Estrada 1991), so far it is impossible to characterize the true impact of rodents on seedling recruitment. Evidence of efficient secondary seed dispersal by agoutis on BCI was reported first by Forget and Milleron (1991) after creating artificial seed shadows. In contrast to *Virola*, lack of post-dispersal parasitism in *Brosimum* allows unburied seeds to germinate and develop as viable seedlings; nine out of 14 marked seeds had germinated within 4 weeks (P.-M. Forget & T. Milleron personal observation). Rodent species still play a potential role as secondary seed dispersers of insect-free seeds whose dispersal may be inefficient when buried seeds fail to establish.

This study shows that the removal as well as the fate of *Brosimum* and *Virola* seeds, especially the probability of seed caching, may change radically at a very small spatial scale (several hundred metres across a given forest) among habitats, apparently in relation to density of larger rodents. This suggests that either the same or different levels of seed removal, as a function of distance to a parent tree (Howe 1993, Burkey 1994) or habitat type (Burkey 1993, Osunkoya 1994, Asquith *et al.* 1997), overlap with contrasting seed-fate pathways. As shown for *Dipteryx panamensis* in the dry season (Forget 1993) and in a contrasting way to *Virola*, it is possible that the edible seed of *Brosimum* (and also *Licania*, see hereafter) is a preferred food item that has a high probability of being consumed by rodents when alternative food sources become rare. *Brosimum* may be hoarded more frequently when rodents have enough to eat, extra uncached food being eventually consumed by other vertebrates which usually compete with rodents for food (Smythe 1986). Habitat characteristics, such as the density of fruit trees (Schupp 1992, see also Forget 1992) and crop size (Howe 1993), and seed attributes possibly influence how agoutis would be triggered to eat and/or bury seeds. High seed removal in *Brosimum* should relate to either high predation or secondary dispersal whereas low or high seed removal in *Virola* should be a good indication, respectively, of weak or pronounced secondary seed dispersal by rodents.

Change in seed fate: large-sized seeds

In July, removal of both *Licania* and *Gustavia* seeds was almost 100% within 2 and 4 weeks, respectively. There was a significant effect of species on seed fate (eaten: $F_{1,18} = 36.68$, $P < 0.0001$; cached: $F_{1,18} = 19.68$, $P = 0.0003$; lost: $F_{1,18} = 6.65$, $P = 0.0189$). A greater proportion of *Licania* seeds were eaten at the agouti-rich area (69%) than at the agouti-poor area (40%), and conversely for the proportion of seeds cached (Fig. 2.4). No differences occurred in the proportion of *Gustavia* seeds within each seed fate category between habitats, caching being always dominant and predation lowest. The large nutrient-rich *Gustavia* seeds were more often buried than the less rewarding *Licania* seeds, for which the levels of predation were dependent on habitat and agouti density.

In contrast to the July experiment, 99% of *Licania* seeds deposited in early August were removed within 12 h. The effect of the interaction of habitat and month on seed fate was significant (eaten: $F_{1,36} = 10.69$, $P < 0.0024$; cached: $F_{1,36} = 6.41$, $P = 0.0158$; lost: $F_{1,36} = 9.46$, $P = 0.004$). Overall, less seeds were eaten in August (36%) than in July, and the proportion of

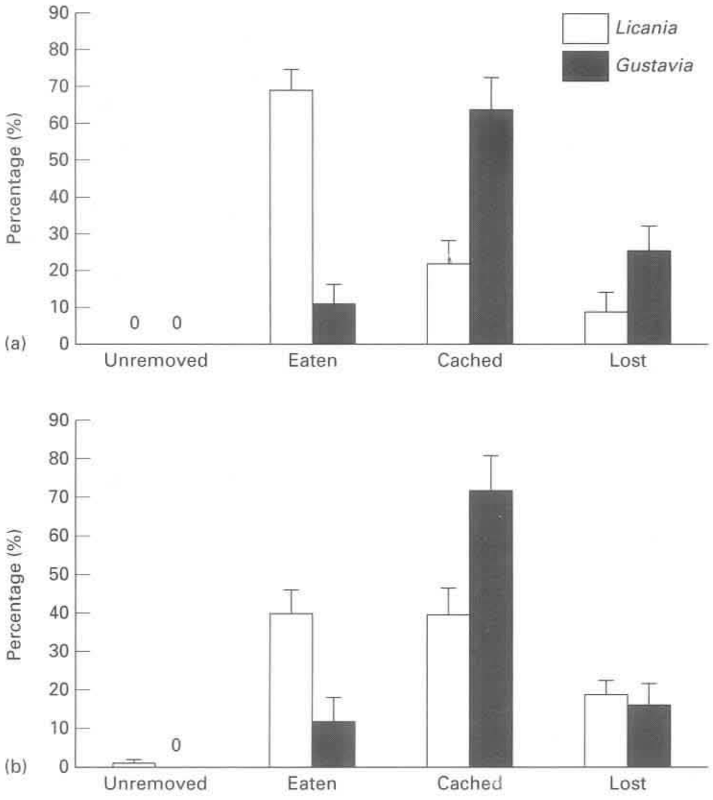

FIG. 2.4. Percentage of seeds (20 sites × 10 seeds) unremoved and the fate (eaten, cached or not retrieved within 10 m: lost) of removed seeds of *Licania* and *Gustavia* in July 1990 at (a) the agouti-rich area and (b) the agouti-poor area along along the R.C. Shannon Trail on Barro Colorado Island, Panama. Bars = 1 SE of mean.

cached and lost seeds changed between July (22 and 9%, respectively) and August (32 and 30%, respectively) at the agouti-rich area. Differences were not very marked at the agouti-poor area. Overall, a greater proportion of seeds were lost in August (33%) than in July (14%). A renewed interest of rodents for fallen nutrient-rich *Scheelea zonensis* seeds in late July–early August (Forget *et al.* 1994), when available food declined at the community level, can explain our results. Interpretation of differences in *Licania* seed fate, however, remains obscure without additional knowledge of the fate of unretrieved seeds that may have been transported greater distances (either eaten, larder- or scatter-hoarded) and without precise data of the alternative food resources in each habitat and period.

Removal of *Gustavia* seeds was marginally greater in July (100%) than in June (88%) ($F_{1,36} = 4.37$, $P = 0.043$). There was a significant effect of month on the level of seed predation ($F_{1,36} = 6.83$, $P = 0.013$). Overall, the proportion of seeds per fate category differed significantly ($F_{2,54} = 67.7$, $P < 0.001$). The proportion of seeds eaten was 10-fold greater in late July (12%) than in late June (1%). There was no effect of habitat on survival of cached seeds at agouti-rich and agouti-poor areas (14 and 11% in October 1990, respectively). There was a trend for greater survival of seeds cached in June (17.6) vs. July (8%), but the difference was not significant ($G = 3.47$, df = 1, $P > 0.05$).

As previously observed for smaller seeds, seed attributes may influence seed fate. The fresh *Licania* seeds were more often consumed than the non-germinated *Gustavia* seeds, the latter being almost exclusively cached. Difference of toxicity between seed species may explain such an outcome (see Forget 1992). In *Gustavia*, burying seeds may allow cotyledons to detoxify with, for instance, translocation of seed toxins to roots, stems and leaves. As with *Dipteryx panamensis* (Forget 1993), *Licania* falls within a bat-fruit dispersal syndrome and is also dispersed by agoutis following seed transportation by bats. Many other large-seeded bat-dispersed species could be also dependent on scatter-hoarding rodents for successful regeneration, especially when seeds are attacked by post-dispersal invertebrate predators as in the case of *Andira inermis* (Janzen, Miller, Hackforth-Jones *et al.* 1976). The lack of difference in *Gustavia* is consistent with the hoarding and survival rates of cached seeds shown for the *Gustavia*-rich area (Forget 1992). This suggests that when agoutis are present to disperse seeds, habitat features influence survival probability of cached and germinating seeds more than scatter-hoarding rate alone. Changing behaviour, especially agonistic behaviour between males and females (Smythe 1978, see also Korz *et al.* 1996), is likely to alter rates of seed caching between plant species and habitats from one month to another depending on overall food resources. In forested habitats with few or no dry season, key resources such as *D. pana-*

mensis seeds (De Steven & Putz 1984, Forget 1993) and previously buried palm nuts (Smythe 1989) supporting a persistent population of agoutis (Adler & Seamon 1991), a much greater proportion of seeds should be eaten instead of being cached immediately after seed fall.

PERSPECTIVES AND RECOMMENDATIONS

The morphological traits of seeds are important in shaping seed removal rate and loss (e.g. Willson 1988, Osunkoya 1994, see also Dirzo & Dominguez 1986) as well as seed fate. In this study, we provide evidence that caching rate tends to increase with seed weight (Fig. 2.5). A similar experiment by Hallwachs (1994) in a different neotropical forest showed the same relationship, implying that removal cannot be attributed to predation when seeds weigh more than 1 g. Indeed, Hallwachs (1994) brought to light new aspects of the scatter-hoarding behaviour of the agouti (*D. punctata*). She carried out several experiments across seasons to determine the food reward per piece of coconut transported, and consumed or cached by agoutis. The study clearly showed that (i) agoutis ate proportionately less of a food item as item weight increased; and (ii) the distance a 'seed' was carried and cached increased with weight of the food reward. 'Seeds' as small as 0.5 g were mostly cached within 5 m whereas mean distance for those cached items of 1–3 g was 6–7 m and much further for 6–30 g 'seeds'. A seasonal contrast was also highlighted by Hallwachs (1986) which agrees with Rankin's (1978) suggestion that rodents might eat proportionately fewer seeds and

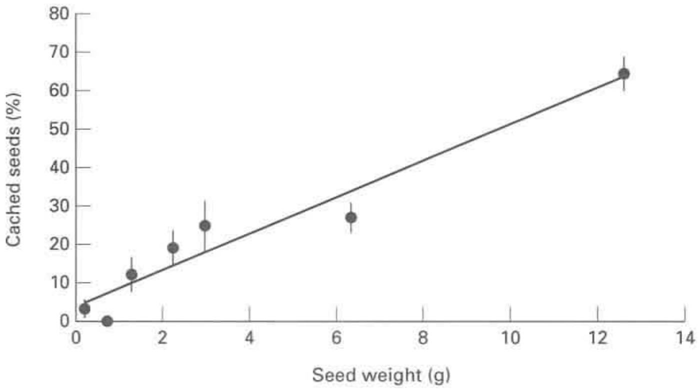

FIG. 2.5. Relationship between seed weight and mean (± SE) percentage of retrieved seeds cached within 5 m (seed <3 g) and within 10 m (seed >3 g) of the sites. Data for *Licania* (6.3 g) and *Gustavia* (12.3 g) are means for 2 month study periods. (Percentage of seeds cached = 4.85 × seed weight (g) + 3.47, $r^2 = 0.938$, $F_{1,5} = 75.7$, $P < 0.001$.)

cache more in the wet season than in the dry season. Not only does seasonal rainfall account for such a contrast, but caching may be low either in the dry season (Forget 1993) or in the late wet season (Forget *et al.* 1994; this study) depending on fruit availability (Smythe 1978).

Future studies should test the relationship between carrying distance and weight of food reward (Hallwachs 1994) considering animal home-range size and seasonal use of its foraging area. When food is scarce in the dry season, agouti may forage in another animal's area (thus increasing temporally the local rodent density, see Forget 1993) and carry fruits and seeds hundreds of metres (Hallwachs 1986) before returning to its home range. Conversely, they may transport seeds of a nearby food source (within several tens of metres) when food is locally plentiful in the wet season (Hallwachs 1986, Forget 1990, 1996). A better estimate of caching rates by reducing the lack of determination of seed fate (i.e. lost seeds) implies an adjustment of the searching radii dependent upon seed size. When there are several artificial seed piles per habitat, we recommend searching for marked seeds within 10 m for small ones *c.* 1–3 g, and at least 20 m for larger ones. If time is available, then it would be highly preferable to search at greater distances (e.g. 30–50 m). The category of lost seeds often comprises cached seeds that are not detected given the searching effort, but they may also be larder-hoarded by small rodents. If one may assume that caching rate and distance depend on the rodent species, then semi-permeable exclosures are recommended to discriminate the role of the small nocturnal species (Terborgh *et al.* 1993) especially when considering small- to medium-sized seeds. Given the wide range of seed size that nocturnal rodents consume (Guillotin 1982, Adler 1995) and maybe cache, checking marked seeds at dawn and dusk is also informative (Vandermeer *et al.* 1979, Forget 1991).

Post-dispersal seed fate is especially critical for those plant species whose successful seedling establishment rate is closely correlated with caching and incomplete cache recovery (Price & Jenkins 1986, Vander Wall 1990). A high percentage (nearly 100%) of post-dispersal predation is not surprising and should be viewed as a common picture given that rodents mostly rely upon these caches to survive when food is scarce; it may be the price of truly effective seed dispersal (i.e. dispersal giving rise to seedlings). On the other hand, a small percentage (1–10%, or less) of cached seeds escaping predators may match a large number of successfully established seedlings when the dispersed crop is large (>1000–10 000 seeds per tree). The most reliable way to validate the hypothesis that rodents are reliable seed dispersers is with labelled seed studies through the post-germination phase. A variety of techniques to trace removed seeds and fruits have been successfully used, including radioactive-labelling (Abbott & Quink 1970, Vander

Wall 1994, 1995), metal (Sork 1984) and magnet-tagging (Alverson & Diaz 1989), thread-tagging (Hallwachs 1986, Forget 1990, Iida 1996, Soné & Kohno 1996) and tracing with fluorescent pigments (Longland & Clements 1995). Ultra-light radio-transmitters (Soné & Kohno 1996) may also help to increase successful retrieval of cached seeds at distances far from their sources, but their current cost is prohibitive when large samples of seeds are required. The same methods as those used for following early seed fate may be used to estimate the rate of recovery of seeds by animals, and possibly recaching. All methods have the same disadvantage. Given the high rate of cache use by animals, the limited number of labelled seeds (several hundreds to thousands) prevents study of a large number of naturally buried seeds through to the seedling stage, when the marking itself does not prevent successful germination and establishment. Among these methods, the thread-marking method is cheap since it does not require special sophisticated equipment, is easy to apply using a drill, thread and good eyes to located cached seeds, and provides rapid recording of immediate seed removal and fate.

When natural caches are too scarce due to high post-dispersal predation, experimental but realistic burial must be used based on field observations of rodent behaviour; that is, spacing buried seeds around focal trees (phase I of seed dispersal *sensu* Chambers & MacMahon 1994), and at greater distances (to several hundred metres) simulating secondary seed dispersal (phase II). This last method presents a bias because the memory component of cache recovery is eliminated. Locating buried seeds at particular microsites (Willson 1988) where rodents hoard food (i.e. near logs, branches and at the base of palms and trees, see Kiltie 1981, Forget 1990), would be even better in order to simulate animal caching behaviour, and in this way reduce bias. Such an approach also has the advantage of testing the effect of burial on germination and seedling establishment and the effect of others predators (insects, peccaries) depending on microsite location such as gaps and shaded understorey (Schupp 1988a, Willson 1988, Schupp & Frost 1989, Osunkoya 1994).

Seed fate in the understorey may differ from that in gap openings. To understand the contrast in habitat choice between seed and seedling (Schupp 1995), one may assume that seeds removed in gap openings by rodents are recached within that environment. Thus, besides the degree of canopy openness, it is maybe the dense tangle of dead branches and logs (often associated with canopy disturbance), that favours survival of cached seeds which most likely establish and grow when gaps are sunny (see Schupp 1995). For instance, this is more probable for medium-sized seeds (*c.* 2.9 g) such as those of *Welfia georgii* (Schupp & Frost 1989) than for smaller-sized seeds (*c.* 0.3 g) such as those of *Faramea occidentalis* (Schupp 1988a).

Like morphology, plant phenology is another crucial parameter influencing the seed-fate pathway. Hoarding seems to be regulated by food abundance as suggested by experiments in the laboratory (Vandermeer 1979) or in the wild (Forget 1993, 1996). Caching appears to increase as satiation occurs, and cache recovery may be subject to the same ecological factors. Seasonal and spatial contrasts in seed fate are likely to be related to within-year changes of seed availability influencing the foraging, hoarding and feeding activities of rodents (Vandermeer *et al.* 1979, Forget 1993, Forget *et al.* 1994). Replicated experiments in space across the forest and in time throughout the fruiting season associated with standardized measures of resource availability at the community level, such as the number of fruiting trees and species and the average fruit/seed biomass falling on the ground, are thus essential. Because these parameters are likely to fluctuate annually, the net effect of rodents will therefore depend on the frequency of good and bad years; that is, years in which seed predators are or are not satiated (Janzen 1970). These considerations argue for more caution in drawing conclusions from short-term studies and for making longer periods of observations (i.e. 4 years for annual species, as in Schupp 1990; and ≥10 years for masting species).

Finally, the choice of habitats for experiments (natural or disturbed, entire or fragmented, with or without edge effects, hunted or not) largely condition the results. In Central America, for instance, long-term consequences of forest fragmentation on the populations of vertebrate predators (Estrada *et al.* 1994, Wright *et al.* 1994) have altered the level of seed removal and predation by rodents (De Steven & Putz 1984, Sork 1987, Forget *et al.* 1994, Hoch & Adler 1997) and by insects (Janzen 1971b, Janzen *et al.* 1976, Bradford & Smith 1977, Herrera 1989). Any change in the level of secondary seed dispersal as a function of habitat and rodent population density may have critical consequences on spatial distribution and survival of seeds and seedlings, and possibly on the maintenance of tree diversity (Leigh, Wright, Herre & Putz 1993).

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